Unique feeding mechanism defines foraging duration and location in the largest marine predators

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The blue whale (*Balaenoptera musculus*) and the fin whale (*B. physalus*) are the largest predators on earth. Adults average 24.7 and 21.2 m in length, and 92,671 and 52,584 kg in weight, respectively[1]. Although large body size usually extends dive duration in air-breathing vertebrates[2], these two large species perform short dives for their size[3] (Fig. 1). Two hypotheses may explain this paradox: the foraging behavior of these whales is metabolically expensive or prey are always located in shallow water and disperse quickly during foraging bouts. Optimality models and remote-sensing techniques (time-depth recorders or TDRs) were used for the first time in these species. They demonstrate that lunge feeding at depth reduces foraging dive duration due to exceptionally large energetic costs associated with this unusual feeding behavior. Consequently feeding by these enormous mammals is confined to short durations of submergence and to areas with dense prey aggregations. As a corollary, blue and fin whales may be particularly vulnerable to perturbations in prey abundance.

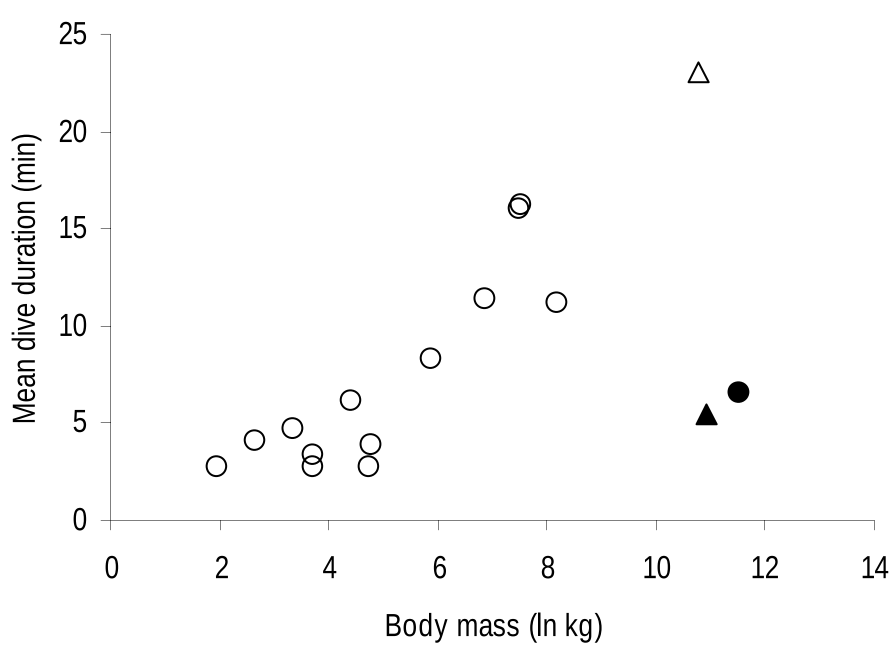


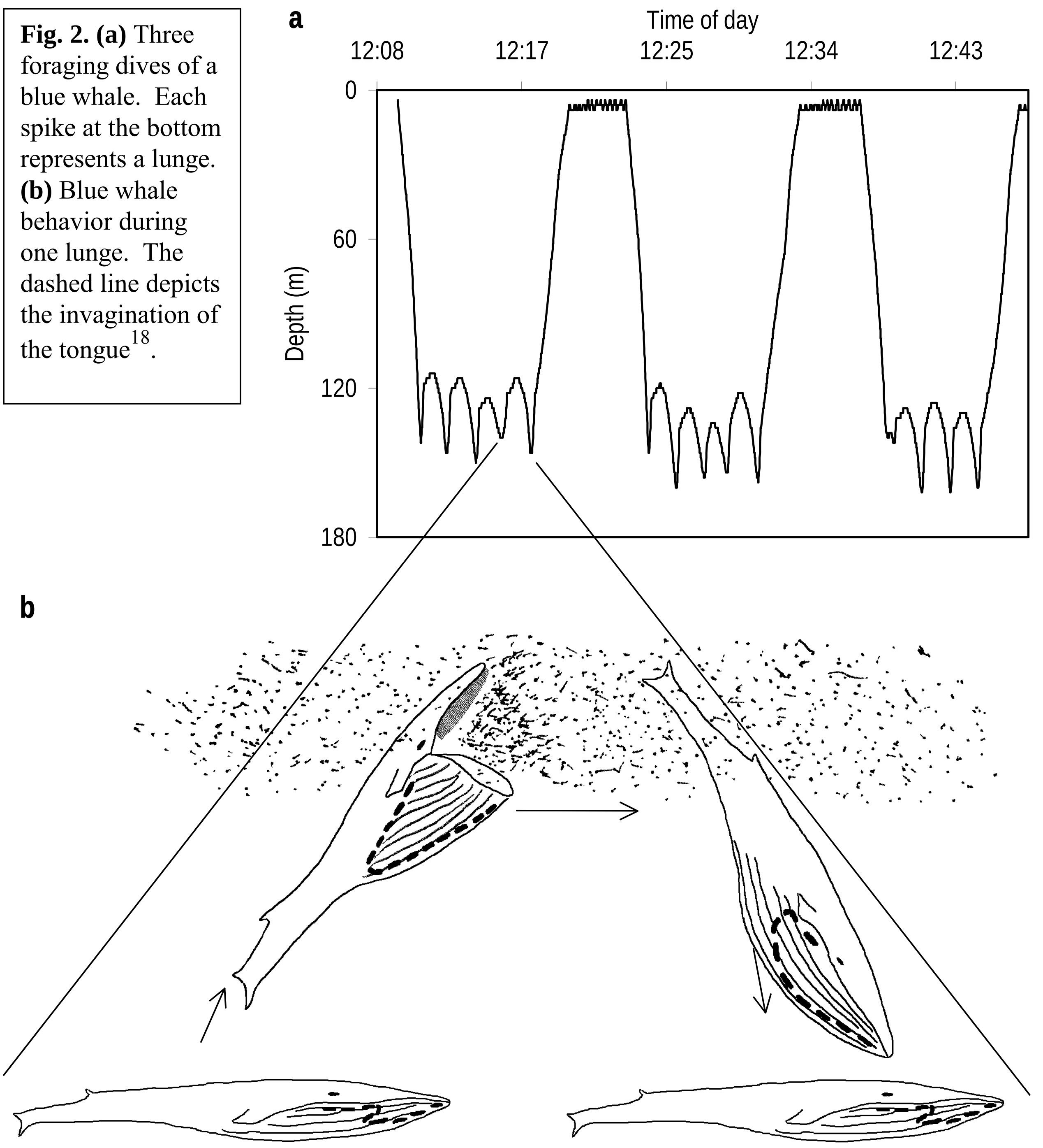
Fig. 1. Blue and fin whales perform short dives for their size. Body mass and dive duration of species diving to an average depth of 80 - 150 m. Solid circle: blue whale; solid triangle; fin whale; open triangle: bowhead whale (*Balaena mysticetus*); open circles: different seabirds and marine mammals[3].

Large body size allows air-breathing vertebrates to increase their oxygen stores and thus prolong foraging duration underwater[2]. Because oxygen is a limiting factor some marine mammals, including blue whales, glide during a dive to reduce oxygen consumption[4]. The theoretical aerobic dive limit (TADL) measures the time that a diver is able to remain underwater relying solely on its oxygen stores[5], and is calculated by estimating the oxygen stores and diving metabolic rate of a species, usually based upon body mass[6]. The TADLs of blue and fin whales are 31.2 and 28.6 min, respectively, yet their foraging dives average only 7.8 and 6.3 min[3]. Although short dive durations are expected when prey are found in shallow water[7], blue and fin whales forage at depth[3]. To explain the discrepancy between measured and predicted dive durations in blue and fin whales, we evaluated cost of lunge feeding by attaching TDRs to seven blue and eight fin whales and prey dispersal by plotting the locations of the tagged whales when foraging.

Blue and fin whales feed by lunging forward to engulf water containing elusive prey: small (<4 cm) euphausiid crustaceans and, in fin whales, schooling fish[8]. Prey items are filtered through keratinized plates called baleen[8]. When lunging, the mouth and throat engulf a mass of water representing nearly 70% of the whale's body weight per lunge[9] (Fig. 2). The fast forward swimming motion of the whale and the displacement of the tongue, which invaginates to form a hollow structure, force water and prey into the mouth[10]. After euphasiids are engulfed, the lower jaw is closed and water is forced through the baleen[9]. When feeding at the surface whales breathe immediately after each lunge; however, when feeding at depth they lunge up to eight times before coming to the surface to breathe[3]. The sudden acceleration of a 90-ton body and the abrupt increase in drag due to the open mouth moving against the water is termed "the largest biomechanical event on earth"[11]. While lunging presumably incurs a large metabolic cost, this has not been measured.

We examined if lunging is energetically expensive with optimality models that employ foraging duration at different water depths as currency[7]. Although optimality models

Fig. 2. (a) Three foraging dives of a blue whale. Each spike at the bottom represents a lunge. **(b)** Blue whale behavior during one lunge. The dashed line depicts the invagination of the tongue[18].



have been successfully employed to study small divers[5], they have not been applied to the largest species. Since animals need more time to replenish their oxygen stores as the cost of a dive increases[12], we examined the prediction that recovery rates of blue and fin whales after a dive are positively related to number of lunges per dive normalized for dive duration. In this is true a cost-of-lunging model should provide the best fit to the observed dive durations. The short dive durations of blue and fin whales could also be explained by the dispersal of prey. Because whales feed upon dense aggregations of euphasiids[13-14], foraging bouts should last for one dive before whales move elsewhere and the distance between foraging dives should be greater than the size of dense euphasiid aggregations.

We found that lunging is energetically expensive and apparently limits dive duration in blue and fin whales. Post-dive surface intervals increased rapidly with increasing number of lunges per dive normalized for dive duration (Fig. 3a). Absolute differences between predicted and observed dive durations were smallest in the cost-of-lunging model for dives with two or more lunges (Fig. 3b). However the cost-of-lunging model did not explain dives with one lunge better than the no-cost model. Apparently this is because whales exerted the least effort per lunge when lunging once. Lunge velocity and distance increased in blue whales from 1.5 ± SD 0.90 $m \cdot s^{-1}$ and 24.0 ± SD 11.37 m in dives with one lunge to 2.6 ± SD 0.95 $m \cdot s^{-1}$ and 34.7 ± SD 8.07 m in dives with two or more lunges, respectively (paired *t*-test, distance: $t_{(5)} = -2.80$, $P = 0.027$; velocity: $t_{(5)} = -4.47$, $P = 0.007$). Likewise, lunge velocity and distance increased in fin whales from 1.5 ± SD 0.37 $m \cdot s^{-1}$ and 17.3 ± SD 6.57 m to 1.8 ± SD 0.31 $m \cdot s^{-1}$ and 23.3 ± SD 2.83 m (paired *t*-test, distance: $t_{(5)} = -2.39$, $P = 0.048$; velocity: $t_{(5)} = -2.61$, $P = 0.035$). Thus we suggest that dives with one lunge represent exploratory dives in which whales assess if the concentration of prey is large enough to warrant foraging. Such foraging thresholds appear to occur in blue whales[14-15].

Our observations do not support the prey-dispersion hypothesis because whales remained foraging in one area (~ 2 x 2 km) for extended periods of time, indicating that they were foraging on the same aggregation of euphasiids[14]. Foraging bouts were comprised of 9.1 ± SD 8.90 and

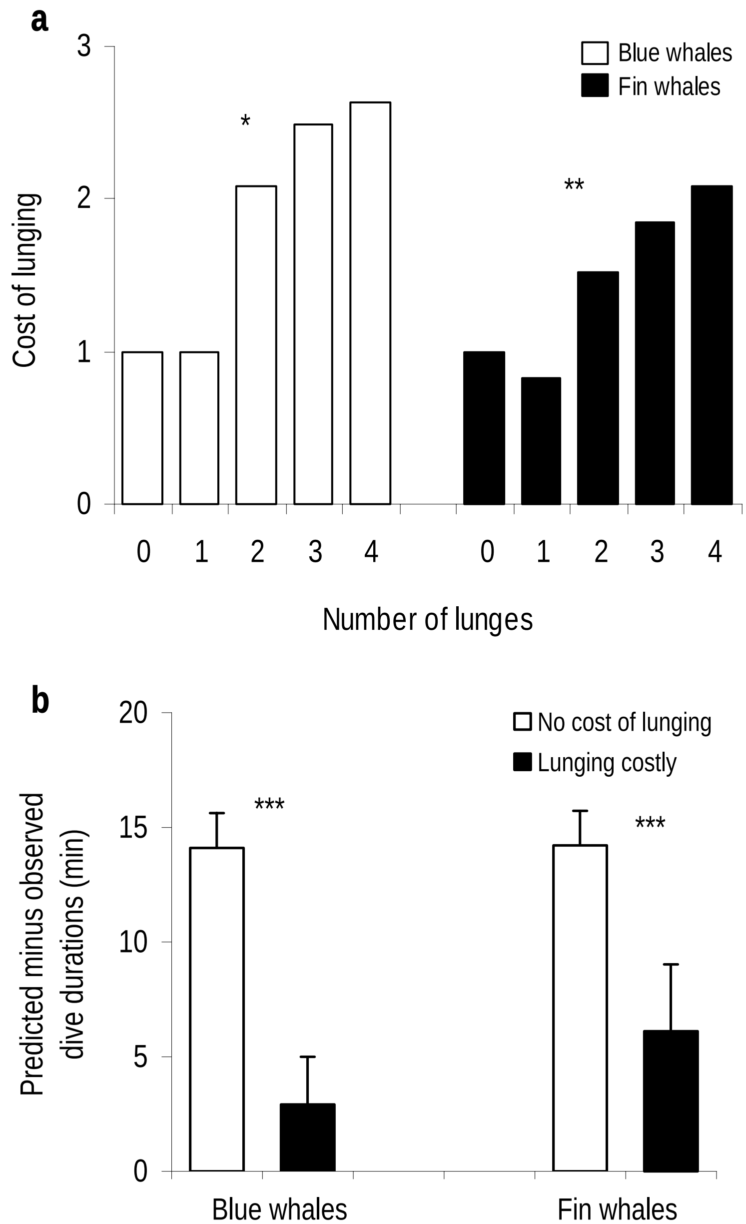


Fig. 3. Results support the cost-of-lunging hypothesis. **(a)** Cost of lunging increased with number of lunges per dive (Order of heterogeneity test[19], OH = 0.57 and 0.67 in blue and fin whales, respectively). **(c)** The cost-of-lunging model was the best predictor of dive duration for dives with two or more lunges (*t*-test, for all dives $P < 0.001$). Thus we combined those dives in the graph for clarity. For all graphs: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, error bars indicate SDM.

10.9 ± SD 10.15 dives, and the distance between foraging dives averaged 525.4 ± SD 144.98 m and 895.7 ± SD 198.09 m in blue and fin whales, respectively. These values are well within the size of euphasiid aggregations (~5,000 – 10,000 m in one dimension) upon which the whales typically feed[13-14]. In addition, recent studies show that euphasiids maintain dense aggregations for several days, even when whales are foraging in the area[14-15].

Based on our results large whales that do not lunge should dive longer than blue or fin whales. Adult bowhead whales average 48,250 kg in weight[3] (48 % less than blue whales), yet their dive duration is more than three times that of blue whales foraging at similar depths (Fig. 1). A similar pattern exists in pinnipeds: fur seals and sea lions (family Otariidae) have short dive durations due to an energetically expensive foraging behavior, while true seals (family Phocidae) move slowly to maximize dive duration[16].

Lunging is an impressive biomechanical event that comes at a high energetic cost. At the physiological level, it reduces foraging dive duration despite the fact that blue whales, and presumably fin whales, glide during a dive to save energy[4]. At the ecological level, it confines blue and fin whales to areas with dense prey aggregations and may make them particularly vulnerable to perturbations in prey abundance. Paradoxically, the behavior that allows these endangered whales to exploit the patchy and ephemeral resources of the ocean, limits them to short foraging dives in productive regions such as submarine canyons or the Southern Boundary of the Antarctic Circumpolar Current[13,17].

Methods

To test the cost-of-lunging hypothesis TDRs collected data on lunge behavior and dive duration of blue and fin whales. The deployment of TDRs is detailed elsewhere[3]. We define a dive as any period of time underwater at depth ≥20 m and surface interval as the post-dive time at depth ≤2 m. In a profile of time versus depth, an upward movement of 8 m or more followed by a downward movement was tallied as a lunge (Fig. 2). Travel duration was the amount of time that a whale spent moving to and from the surface.

To assess metabolic cost of lunging relative to number of lunges per dive we employed the recovery rate of a dive, i.e. the relationship between dive duration and post-dive interval at the surface. We compared the observed values of dive duration with the values predicted by optimality models assuming either a metabolic cost of lunging or no cost of lunging[7]. The optimal foraging duration was calculated based on equations that maximize foraging duration in divers[7]. The theoretical dive duration of a whale was thus obtained by adding foraging and travel durations[7]. We employed equations [10] and [11][7]:

$$[10]\quad x(s^*) = [K \cdot (1 - e^{(-\alpha \cdot s)}) - (m_1 \cdot \tau_i)] / (\tau + s^*), \text{ defines optimal surface time}$$

$$[11]\quad t^*_i = [K \cdot (1 - e^{(-\alpha \cdot s^*_i)}) - (m_1 \cdot \tau_i)] / m_2, \text{ maximizes foraging time}$$

where K = 31.2 min or 28.6 min, the TADL of blue and fin whales, respectively[3],

α = exchange rate of oxygen at the surface (dimensionless) = 0.5, half the rate of oxygen use while diving[7],

m_1 = rate of use of oxygen while diving (dimensionless) = 1, the proportion of the metabolic rate employed to estimate K[7],

m_2 = rate of use of oxygen while foraging.

For the model assuming no cost of lunging, $m_2 = 1$. For the model assuming a cost of lunging, m_2 = recovery rate of foraging dives (one or more lunges) divided by the recovery rate of a non-foraging dive (zero lunges) = cost of lunging. The recovery rate was defined as the slope of the fitted lines between dive duration and surface interval.

To test the prey-dispersion hypothesis we followed each tagged whale at a distance of 100-200 m from a 15-m vessel and recorded its location at the surface using a GPS. From TDR data we tallied the number of consecutive foraging dives and from GPS data we estimated the distance traveled between each foraging dive.

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